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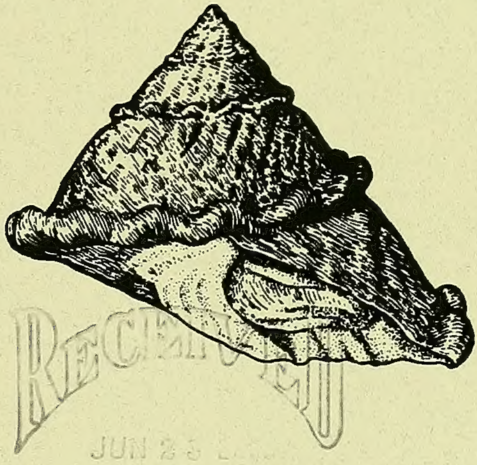
THE WESTERN SOCIETY OF MALACOLOGISTS

ANNUAL REPORT
VOLUME 35



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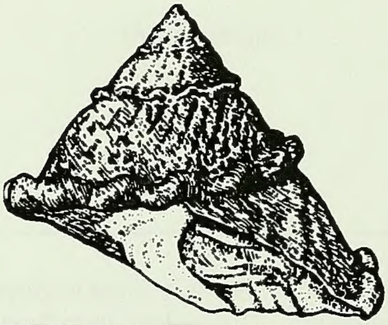

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WESTERN SOCIETY OF MALACOLOGISTS
ANNUAL REPORT FOR 2002, VOLUME 35

Abstracts and Papers from the 35th Annual Meeting of the Western Society of Malacologists held at the Asilomar Conference Center, Pacific Grove, CA, 20-24 July 2002.

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Abstracts and Papers

Experimental taphonomy and the recognition of agglutinated gastropod egg masses in the fossil record

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Many aquatic organisms use sediment to produce agglutinated structures, such as the abdominal cases of caddis fly larvae, tubes of some infaunal polychaetes, and egg masses of some caenogastropods. Despite the abundance of agglutinating organisms and the long phylogenetic history of these clades, these structures have a poor fossil record. Is this the result of a failure of preservation or recognition? There are two key factors for producing a fossilized agglutinated structure: 1) rapid burial to limit decay and degradation and 2) transportation into a sediment type that will permit discrimination between the agglutinated grains and matrix sediment. For sediment-impregnated naticid gastropod egg masses, extensive field collection has revealed that both conditions exist, with approximately 15% of egg masses transported into a different sediment type and 18% partially buried.

Using plaster and various sediment grain sizes, I embedded freshly collected naticid egg masses to create simulated fossils that were used to assess both what a fossilized egg mass would look like and the conditions necessary to recognize them as fossils. The plaster blocks were serially sectioned vertically, horizontally, and obliquely to investigate the variety of forms which may appear in outcrop view. Sections revealed a profusion of unexpected forms dominated by arcs and sinusoidal curves. Egg masses bend as they are buried, yielding uneven thicknesses in these curves. Thickened areas are concentrated at points of reflection and mimic umbonal thickenings seen in bivalve cross-sections. This approach provides a set of search images for the missing fossil record of egg masses.

Large-scale marine ecological studies of the U. S. west coast by the PISCO consortium

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PISCO is a large-scale marine research program that focuses on understanding the nearshore ecosystems of the U.S. West Coast. An interdisciplinary collaboration of scientists from four universities (OSU, UCSC, Stanford, UCSB), PISCO integrates long-term monitoring of ecological and oceanographic processes at dozens of coastal sites with experimental work in the lab and field. We explore how individual organisms, populations, and ecological communities vary over space and time. We conduct extensive fieldwork along some 1,200 miles of the California, Oregon, and Washington coasts, in addition to laboratory experiments at the four universities in the consortium.

The core of PISCO research is a sampling program that combines studies of variability in ocean climate with simultaneous multi-species experimental studies of larval and adult populations over most of the U.S. West Coast. Our research focuses on understanding several broad issues: 1) how currents, upwelling, and other physical and ecological processes affect the plants and animals of coastal marine ecosystems, 2) how coastal ocean ecosystems respond to shifts in water temperature, currents, and other factors that may vary with global climate change, and 3) how ocean circulation affects the dispersal of marine organisms in their earliest larval stages. Examples of several of the large-scale ecological studies within PISCO are illustrated, and some of our preliminary findings and PISCO's potential contributions to molluscan ecology are described.

Are physical factors facilitating marine species invasions?

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The bay mussels *Mytilus trossulus* and *M. galloprovincialis* co-occur from Monterey to Cape Mendocino in a patchy hybrid zone. It is apparent that *M. galloprovincialis* invaded Southern California before 1950 and is currently the only bay mussel south of Monterey. We are interested in whether small-scale physical conditions (temperature and salinity) and differential physiological adaptation can explain the observed patchy distribution of these congeners. To address this question, we have surveyed adult and recruit populations, measured environmental parameters and are testing physiological limits of adults. Scoring individuals using multiple gene loci, we have genetically identified adult and recruit populations in Monterey Bay (MBay) and San Francisco Bay (SFBay). In both systems, we have found that adult *M. trossulus* increases in abundance as one moves up the estuarine gradient (towards higher temperature variability and lower salinity). However, *M. trossulus* has lower heat tolerance than *M. galloprovincialis*, which implies that salinity variation - not temperature adaptation - is driving the observed distribution. We have also found that recruit abundance does not match adult patterns in MBay but does match in SFBay, suggesting that MBay is an open system and SFBay is closed, with respect to recruitment. The mismatch in MBay is largely due to a delayed recruitment pulse of *M. trossulus*, at sites where *M. trossulus* adults are rare or absent. Finally, our results have implications for water resource use and management policies: these policies directly impact coastal communities and could facilitate species invasions when species distributions follow estuarine gradients.

Physical habitat propery mediates biotic resistance to non-indigenous species invasion

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A soft-shelled non-indigenous clam, *Nuttallia obscurata*, has invaded coastal soft sediment habitats of the northeastern Pacific. In a survey of 35 sites within the San Juan Islands, Washington, USA, *Nuttallia* was found almost exclusively in sandy substrates, higher in the intertidal than most native clams (>1m above Mean Lower Low Water). The distinctive distribution of *Nuttallia* suggested that tidal height and sediment composition may be important physical factors that control refuges available to *Nuttallia*, regulating its exposure to predation and ultimately the success of its invasion. I tethered *Nuttallia* for 24 hrs in the high intertidal where it is typically found and in the low intertidal at an elevation where it was never found. Clams restrained to the surface suffered high mortality from crab predation at both tidal heights, whereas control clams with unrestricted movement exhibited high mortality rates only in the low intertidal. In a second experiment I transplanted sediment within and between the two intertidal heights to measure effects of tidal height and sediment type on survival and burial depth of *Nuttallia*.

At both tidal heights all clams placed on mud-cobble substrata, naturally common in the low intertidal, suffered high mortality rates (>60% in 24 hrs). *Nuttallia* on loosely packed sand substrate, naturally found in the upper intertidal, however, survived better because they buried deeper than in the tightly packed mud. Caged control clams at both tidal heights suffered no mortality. Apparently, native predators are mitigating community level impacts of an invader by excluding *Nuttallia* or relegating it to a zone not often inhabited by native species, thereby reducing potential competitive interactions. These findings illustrate that a physical characteristic can mediate biotic resistance to an invader and thus control invasion success and community-level impacts. Generally, such physical-biological interactions may explain some of the reported site-to-site variability in invasion success.

Marine biodiversity of mollusks in Costa Rica: The case of Opisthobranchia

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Since 1994, the National Biodiversity Institute (INBio) in Costa Rica has been conducting an inventory of marine mollusks along both the Atlantic and Pacific coasts of Costa Rica. Several international experts have contributed significantly to improve the knowledge of the different groups of marine mollusks. INBio personnel and collaborators have hosted several fieldtrips and workshops to different Marine Reserves and National Parks in order to train curators, technicians and parataxonomists in collecting techniques, preservation, and identification of the different groups. An overview of the results of the inventory including some of the 142 new records and 19 new species of opisthobranchs collected along both of the country's coasts are presented. Some of the biogeographical implications of these records are also discussed.

The significant role of epilithic biofilm as a food resource for intertidal grazers, *Siphonaria japonica*

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Hong Kong rocky shores are covered with a cyanobacteria-dominated epilithic biofilm throughout the year. As the base of the benthic food chain this biofilm is the principle food source for all intertidal grazers. This resource varies, however, in terms of species composition and distribution. Multivariate analysis of their nutritional value showed unicellular species to be lipid-rich and filamentous forms to be protein-rich. The influence of variation in biofilm species richness and abundance on the life history dynamics and diet of a limpet, *Siphonaria japonica*, was investigated. This pulmonate lays benthic egg

masses and is annual on most Hong Kong shores. As such, this species is an ideal organism to measure short-term impacts of diet on life-history traits. Under laboratory trials the limpet preferred protein-rich filamentous cyanobacteria species. On shore, gut content analyses also revealed that the limpet preferred these species during their growth and reproductive period. The role of cyanobacteria driving rocky shore food webs was also indicated by the positive correlation between cyanobacteria biomass and growth rates of *S. japonica* over an 18-month study. The growth rate of *S. japonica* on shores dominated by filamentous cyanobacteria was faster than for shores dominated by unicellular cyanobacteria and other algae. *S. japonica* also invested more energy into gonad development and laid more and larger egg masses on shores dominated by filamentous cyanobacteria. These results highlight the significant role of cyanobacteria as primary producers in the intertidal food web and suggest that herbivore fitness can be enhanced by maximizing intake of these high-protein organisms.

Feeding preferences and assimilation efficiencies in the herbivorous marine snail *Lithopoma undosum* (Turbinidae)

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Many studies have examined factors that contribute to food choice in herbivorous marine invertebrates. However, few have considered relationships between preferences and the assimilation efficiencies of food items. The purpose of this research is to establish a preference hierarchy among seaweed foods for the herbivorous marine snail *Lithopoma undosum*, and then to test the hypothesis that preferred seaweeds are assimilated at higher efficiencies than less preferred seaweeds. Differential consumption of seaweeds during three sets of two-choice experiments showed that *L. undosum* exhibits clear feeding choices, preferring kelp species over nine other non-kelp macrophytes. Clear preferences could not be detected among the kelp species tested. Following kelp, the fleshy red alga, *Pterocladiella capillacea*, was preferred over other species of macrophytes, followed by the calcified coralline *Lithothrix aspergillium*, which was preferred over two known chemically defended species and the seagrass, *Phyllospadix torreyii*. Assimilation efficiencies are now being quantified using an ash marker method. Results to date indicate that *L. undosum* prefers kelps over all other seaweeds, but also exhibits defined secondary preferences among less-preferred seaweed foods.

Recruitment and Abundance of Unusual Hydrobiid Snails among Restored and Reference Brackish Marshes of San Francisco Bay Estuary

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Marshes are being restored to various degrees of tidal action in the San Francisco Bay Estuary, Northern California. For three years, we have monitored aquatic animal populations in seven restored and reference (historical and pre-restoration) brackish marshes in southern Suisun Bay. Non-destructive sampling occurred approximately monthly using refugia samplers, which were mesh minnow traps representing a total area of 1 m^2. Two to four traps were placed near emergent vegetation located near the mouth of major tidal creeks in both the reference and restored marshes. Most of the brackish marsh areas were near 38° 3.0' N 122° 3.5' W.

Unusual hydrobiid snails colonized and became common in refugia traps in two of the marsh sites restored to increased (but still muted) tidal action with ponds, and in one small pond isolated from tidal action. These snails ranged from 0.25 to 5.00 mm in shell length. The snails have white patches on the cephalic tentacles and appear to be a close relative of *Tryonia imitator,* an endangered California brackish water snail. Samples have been sent to molluscan authorities for identification. One expert noted that several species could be present. It is possible that one species is a morph of *Hydrobia andersoni,* which is known only from variable fossil specimens several million years old, from up the adjacent, ancient San Joaquin River.

The recent restoration site, Waterfront, was restored to 1.0 -1.5 m tidal amplitude in ~1995 and has a small pond (< 20 m wide) at the end of a 2-km long channel. The older restoration site (Weir Pond, 1 km away) has more muted tidal action of 0.5 - 1.0 m and restoration of tidal action occurred through natural erosion of a man-made levee approximately 10 to 20 yrs ago. Weir Pond, 100 m wide, is located on a small channel in a complex of marshes restored to tidal action.

The hydrobiid snails also colonized the refugia traps at a pond isolated from tidal action within the nearby Navy Pond, which is 2 m wide. In over three years of simultaneous monitoring, these snails were not found in other reference marshes or in the restored marshes lacking ponds.

Average seasonal densities of the snails from the refugia traps between 1999 and 2002 revealed a patchy snail distribution among sites and an apparent crash, followed by recolonization at the Waterfront site (Fig.1).

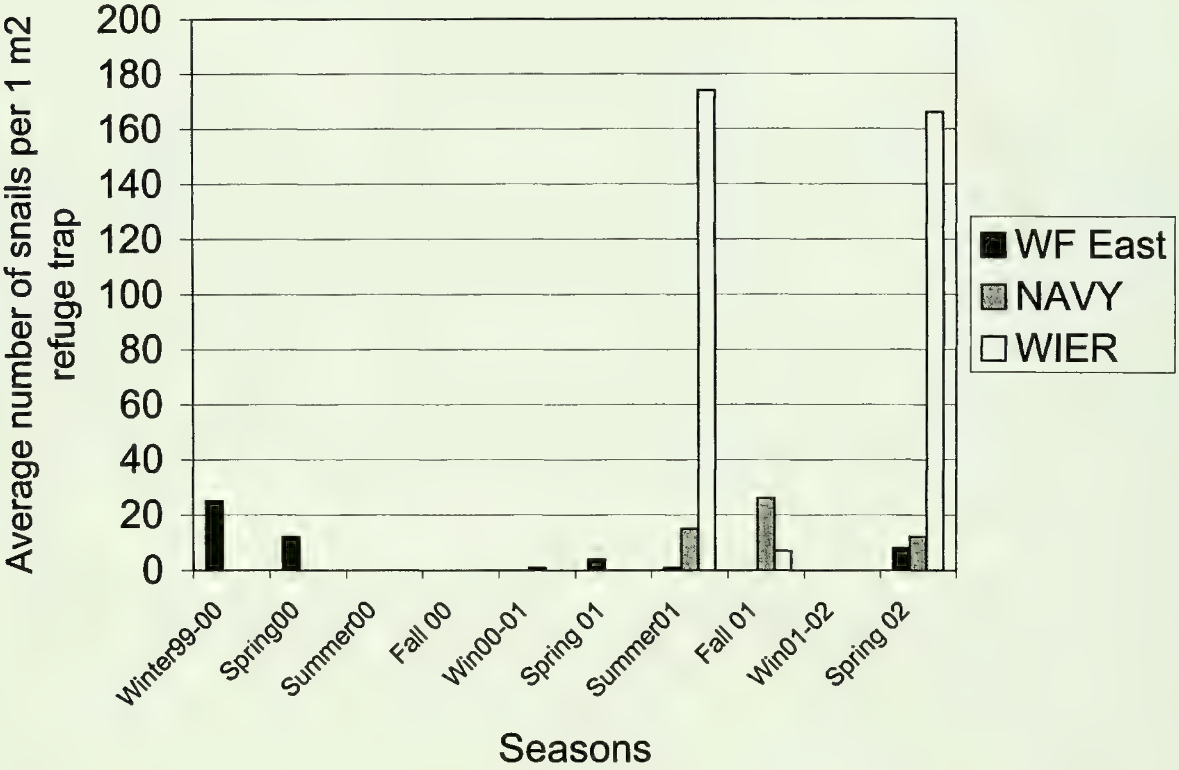

Figure 1. Snail populations sampled seasonally with refugia traps at several sites in Suisun Bay, northern San Francisco Bay.

Sampling with the refugia traps began at the older restoration marsh, Weir Pond, after we located it in 2001. Highest average seasonal densities occurred at this site in summer, 2001 (Fig. 1), averaging 174 ± 206 (SD) snails per m^2. Visible densities of these snails were so high at this site that circular mini-quadrats representing an area of 25 cm^2 were employed in four replicates along the shore on a 20 m transect. These quadrats yielded an average density of 212 ± 187 (SD) snails per 25 cm^2, and an average of 60 ± 33 (SD) snails per 25 cm^2 in vegetation dominated by *Enteromorpha* algae (Fig. 2). For comparison, similar sampling occurred at the recently restored Waterfront site (the pond at the west end of the 2 km channel), yielding averages of 3 snails per 25 cm^2 in the mud and 2 snails per 25 cm^2 in vegetation.

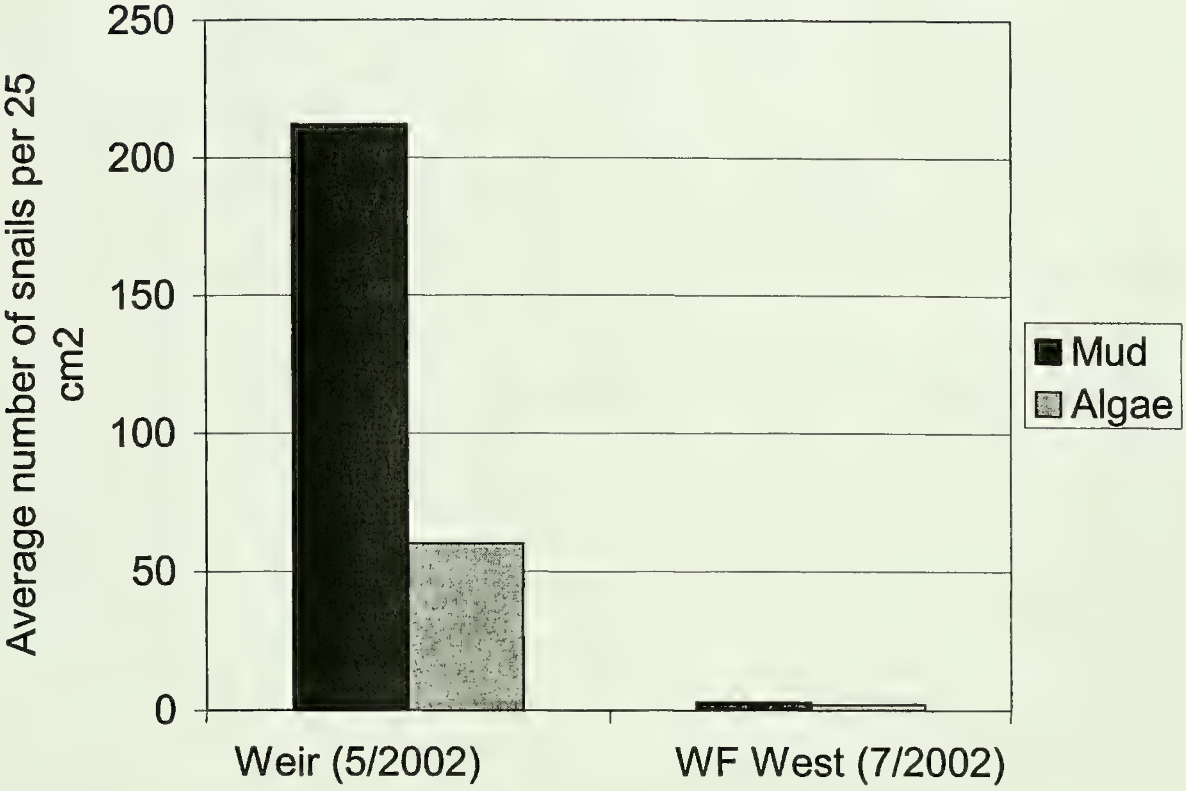

Figure 2. Snail populations sampled during early summer with mini-quadrats at two restored marshes with ponds.

In our laboratory observations, and in later field collections, these snails appeared to brood their young, with females releasing at least 5 -10 young at the approximate juvenile shell length of 0.25 mm. These juveniles reached a shell length of between 1 and 1.25 mm in nine months. Also, no new recruits had reproduced at this time. Adult snails survived gradual fluctuations in salinity of 6 - 42 ppt (20~120% seawater), with no mortality. The snails were observed feeding on filamentous algae, including cyanobacteria and diatom chains.

Throughout the study, marshes without ponds, both restored and reference, yielded none of these common invertebrates and yielded other aquatic invertebrates and fishes at significantly lower densities than at sites with marsh ponds connected to tidal creeks. The substantially higher densities of common aquatic invertebrates at restored sites with ponds, including the appearance of these previously unrecorded snails, adds to the growing evidence that marsh ponds connected to the tidal creeks may play a crucial role in the biological success of future marsh restorations.

Acknowledgements

This work began with a Cooperative Agreement with US Fish and Wildlife Service, funded by the CALFED Bay-Delta Program. We gratefully acknowledge those assisting in this work, particularly J. Rees, and S. McGinnis (additional Co-Principal Investigators), Contra Costa Mosquito and Vector Control (K. Malamud-Roam and L. Hanson), J. Kohler, S. Webster, T. Smith, A. Gaos, C. L. Hamer, Martinez Bait and Tackle, Big Break Marina, and R. Bogaert and the McNabney Marsh Management Committee, and San Francisco Bay Wildlife Society. We also are grateful to James McLean and Robert Hershler, who examined specimens of the unusual hydrobiid snails.

History of the classification of mollusks

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It is quite well accepted today that the Phylum Mollusca comprises nine higher taxa, even if their relationships are still debated. Modern history of the classification of mollusks started with Cuvier who introduced the term Mollusca in its modern sense in 1795. After Cuvier, it took more than one hundred years to obtain the higher groups we accept today: 1) new organisms have only been discovered during the mid nineteenth century, like chaetoderms or solenogasters; 2) zoologists had to get rid of affinities inherited from much older classifications, like the close relationships between Ascidians and Bivalves first suggested by Aristotle. The main changes that occurred in the classification of Mollusks, from Aristotle up to the beginning of the twentieth century, are discussed. These changes are explained through the study of the successive — and very different — historical contexts in which scientists worked.

Limits to optimization: Hydrodynamics, shell shape, and survivorship in the owl limpet, *Lottia gigantea*

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On wave-swept rocky shores, limpets are subjected to water velocities in excess of 20 m/s, which may impose large hydrodynamic forces. Despite the extreme severity of the flow environment, predictions from laboratory experiments on conical models suggest that limpets' shells are far from the optimal shape that would minimize the risk of dislodgment, a deviation that is allowed by the high tenacity of the limpets' adhesion to the substratum. I tested this conclusion using the limpet *Lottia gigantea*. Shells of this species differ substantially from the hydrodynamic optimum in that their apices are displaced anteriorly to form a plow that is used to defend the limpet's territory. The hydrodynamic effects of this shape are similar to those observed in models: the animal experiences an increased lift when facing into flow and a decreased lift when the flow is at its back. However, neither effect has a substantial impact on the risk of dislodgment. When the animal is stationary, its adhesion to the substratum is very strong, and its risk of being dislodged is small despite its sub-optimal shape. In contrast, when the animal is crawling rapidly, its adhesion is substantially decreased, and it would probably de dislodged by rapid flow even if the shell were shaped optimally. The risk of dislodgement by waves is therefore functionally independent of shell shape, and the shell has the 'permission' of the environment to respond to other selective factors, in particular those associated with its aggressive, territorial behavior.

Toxic substances in strange places: Studies on chemicals found in dorid nudibranchs, ecological roles and cytotoxic findings

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Most dorid nudibranchs feed on marine sponges, a phylum of animals with abundant and varied natural products chemistry. Analyses of the mantle and digestive tissues of nudibranchs collected from a wide range of habitats indicate that potent sponge chemicals are disparately sequestered in nudibranch tissues. Possible ecological roles of these chemicals are investigated by examining the effects of the chemicals on ascidian larval settlement, metamorphosis and mortality. Recent cytotoxic studies have been performed on P388 mammalian cancer cells using the crude chemical extract of the nudibranchs. These studies indicate the presence of extremely toxic compounds that are lethal to the cancer cells. Further chemical isolation is underway to determine the identity of the compounds.

Paleoecology of early Triassic Gastropoda and Bivalvia: Understanding molluscan success during the biotic recovery from the end-Permian Mass Extinction

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The end of the Permian is characterized by the most devastating biotic crisis in the Phanerozoic history of life; two mass extinctions eliminated 71% and 80 % of species at the end of the Maokouan and Changxingian stages, respectively. In the marine realm, the Permian/Triassic boundary marks the decimation of the articulate brachiopod-dominated Paleozoic Fauna and the rise of the mollusc-dominated Modern Fauna. The classes Gastropoda and Bivalvia survived the end-Permian crisis better than any other marine invertebrate groups and, during the Early Triassic biotic recovery, marine paleocommunities

were dominated by astronomical numbers of stunted gastropods and bivalves. We have conducted quantitative paleoecological studies on three successive Early Triassic western Pangean seaways in order to understand the ecology of gastropods and bivalves during the biotic recovery from the end-Permian mass extinction.

Results indicate that the adults and juveniles of two microgastropod species dominate a range of Lower Triassic nearshore carbonate paleoenvironments. These gastropods were opportunists that thrived during the environmentally stressful, ecologically relaxed aftermath of the end-Permian mass extinction. The small size of Early Triassic gastropods is attributed to stunting due to abnormalities of global environments during the end-Permian mass extinction's biotic recovery. Results from our regional paleoecological studies also indicate that during the Early Triassic, low-diversity bivalve assemblages dominated nearshore to slope marine depositional environments. It appears that bivalves were engaged in an ecologic takeover, enabling them for the first time to be more diverse and abundant than articulate brachiopods in a wide range of environments.

Morphology, proposed life habits and phylogeny of "*Lithiotis*" facies bivalves

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Following extensive Late Triassic coral-constructed reefs and the aftermath of the Triassic-Jurassic mass extinction, Early Jurassic buildups are rare and constructed primarily by bivalves. The Pliensbachian exhibits a radiation of aberrant pterioid bivalves, the "*Lithiotis*" facies bivalves, which include: *Lithiotis problematica*, *Cochlearites loppianus*, *Gervilleioperna* sp., *Mytiloperna* sp. and *Lithioperna scutata.* These large bivalves (some specimens greater than 60 cm) with bizarre morphologies are ubiquitous in shallow, nearshore tropical waters.

Over 500 specimens of "*Lithiotis*" facies bivalves were collected from study sites (Western North America, Morocco and Italy) or observed in museum collections. Morphology, microstructure and phenotypic variability were examined for each of the "*Lithiotis*" facies bivalves. Morphological measurements include: width, thickness, number of ligamental grooves, width of exterior bands, angle incidence and obliquity. The life habits of "*Lithiotis*" bivalves were assessed by field observations of various morphotypes and orientation of *in situ* specimens. The reef-building bivalves, *Lithiotis* and *Cochlearites*, have upright, stick-shaped growth forms. The other "*Lithiotis*" facies bivalves, *Lithioperna*, *Mytiloperna* and *Gervilleioperna*, lived in lagoonal facies and exhibit a variety of morphotypes.

All five "*Lithiotis*" facies bivalves share microstructures and ligaments common to the pterioid families Isognomidae and the Bakevellidae. *Mytiloperna*, *Gervilleioperna* and *Lithioperna* have a broad-tooth plate and byssal attachment, characteristics of the Bakevellidae. However, *Lithiotis* and *Cochlearites* lack these traits. The "*Lithiotis*" facies bivalves may represent a transitional lineage between the Bakevellidae and the Isognomonidae during the Late Triassic to the Early Jurassic, a time when bakevellids underwent a major evolutionary radiation and the first appearance of isognomonids.

Effects of predator presence on nematocyst uptake in the nudibranch *Flabellina verrucosa* in the Gulf of Maine

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Aeolid nudibranchs maintain functional nematocysts for protection against predators. Nematocysts are sequestered from the nudibranch's cnidarian prey, and selection for incorporation is largely a function of availability in the diet, but other factors may be involved in determining nematocyst preference. I propose that predator presence influences nematocyst incorporation, as nematocysts are a primary defense mechanism for combating predation.

Nematocyst uptake in the nudibranch *Flabellina verrucosa* collected from the Gulf of Maine was examined in response to predators, including the sea star *Crossaster papposus*, the wrasse *Tautogolabrus adspersus*, and the crab *Carcinus maenas*, and compared to uptake from the diet alone. Nudibranchs in individual flow-through containers feeding on a provided hydroid diet were subjected to tanks containing a predator, after which the nematocyst distribution within the nudibranch cerata was examined. Results from the southern Gulf of Maine show the majority of the changes over the experimental period were attributable to diet, but nudibranchs responded to both the cunner *T. adspersus* and the sea star *C. papposus* stimuli by significantly increasing incorporation of microbasic mastigophores, a penetrating type of nematocyst. No differential uptake was seen with *Carcinus maenas*, which is not a known nudibranch predator. Nudibranch specimens collected from the northern Gulf of Maine exhibited similar changes in nematocyst uptake, increasing incorporation of basitrichous isorhizas in response to both *C. papposus* and *T. adspersus*, as well as microbasic mastigophores when exposed to the cunner. Again, no changes in nematocyst content resulted from *C. maenas* exposure. Changes in nematocyst uptake were evident both for predators present in the collection area, and those with which nudibranchs could have had no previous experience for both northern and southern collection sites. Therefore, changes in nematocyst uptake may be determined by long-term co-evolution of nudibranchs with these predators, not by individual exposure to different predatory cues. This study indicates that in addition to diet, *F. verrucosa*, and possibly other aeolid nudibranchs, modulates nematocyst incorporation in response to the presence of potential predators.

Recovering prehistoric distributions in the time of globalization

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Human-mediated invasions of marine organisms can obscure accurate descriptions of native biogeographic distributions. Incorrectly stated native geographic ranges lead to spurious notions of cosmopolitanism or unusual dispersal or vicariance scenarios. Increased recent attention to human-mediated invasions reduces the perpetuation of this problem, yet hundreds of years of unrecognized human transport has produced a large (but poorly known) number of cryptogenic species: those for which native distributions are unknown. Several criteria may be used to reassign species from cryptogenic to introduced categoriesa in a particular region. These include the presence of disjunct populations that span presumed natural dispersal barriers and taxonomic affinity to biota from different geographic provinces. Phylogeographic and population genetic data provide additional criteria. Introduced populations should have phylogeographic affinity to distant populations, and genetic variation should be reduced in the process of invasion. Case studies of molluscan and non-molluscan marine species are presented to illustrate the use of molecular approaches to the identification of introduced species and the inference of their native distributions.

Historical perspectives on categorical rank in the higher classification of mollusks

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The species is the only taxonomic category for which an objective definition exists. What criteria should determine categorical rank at other levels continues to be debated. According to the analysis provided evolutionary systematists, the rank of a taxon is determined by something called the amount of difference. A closer look reveals that taxa have often been ranked on the basis of metaphysics, tradition, and ignorance. Cuvier was largely responsible for the typological interpretation of mollusks as occupying the highest-level of a class-inclusion hierarchy within the animal kingdom. He justified ranking on the basis of physiological criteria. The classes of mollusks nicely reflect his criteria, in that locomotion is reflected in the names: Céphalopodes, Ptéropodes, Gastéropodes, Acéphales (bivalves and tunicates), Brachiopodes and Cirrhopodes. The approach created a kind of Procrustean bed forcing groups into inappropriate positions. It also militated against substantive changes in the system. Taxa have often been assigned a high rank in order to render their position within the system ambiguous, notably in cases of uncertainty about the relationships. Higher classifications have become lists of several taxa with the same rank. Good examples within Opisthobranchia are the ordinal classification that is still largely in use, and Thiele's lists of families within the Cephalaspidea.

Life at the edge: Examination of the northern geographic range limit of an intertidal limpet

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For many terrestrial species the poleward edges of ranges are determined by climate and physiological stress, while the equatorward edge is determined by species interactions. There is substantially less evidence for this paradigm among marine species, while data on intertidal species are too sparse to evaluate the paradigm at all. For species with a planktonic (swimming) larval stage, ocean currents could also determine the location of range limits. The intertidal limpet *Macclintockia scabra* is distributed from Mexico to Cape Mendocino, CA. To determine whether the northern range of *M. scabra* is set by climate, I conducted a transplant experiment of individuals from two sites within the range to four locations spanning the northern range limit. There was no evidence that snails transplanted beyond the range limit performed worse than control snails transplanted within the range. Moreover, survivorship and growth rate increased with decreasing temperature. Concurrent monitoring of larval settlement showed much lower rates of settlement into northern populations relative to more central portions of the range. Taken together, these results suggest that factors controlling larval dispersal are responsible for determining the northern range limit of *M. scabra*, and that physiological tolerance plays a negligible role.

Stable isotope and sclerochronologic analysis of environmental resolution in bivalve mollusk shells: A new approach for environmental reconstruction

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Isotopic and sclerochronologic variability in bivalve mollusk shells provides a robust archive of the environmental conditions experienced during the lifetime of the animal. These variables reflect numerous environmental parameters, including temperature, salinity, and seasonality. Careful cross-calibration of geochemical and sclerochronologic characters permits high-resolution reconstruction of environmental variability. I analyzed stable oxygen isotope ($d^{18}O$) variability from two live-collected specimens of *Chione cortezi* in conjunction with profiles of daily growth-increments and temperature records from the same site. This study facilitated the dating of individual $d^{18}O$ samples, established the maximum and minimum temperature thresholds of growth, and constrained the temporal resolution of individual isotope samples. This analysis indicates that shells of *C. cortezi* from the northern Gulf of California do not contain a complete record of annual environmental variability. Modeled $d^{18}O$ profiles further define the fidelity of isotopic and sclerochronologic based reconstructions with respect to observed environmental variability. Modeling results and observations indicate that the fullest range of environmental conditions is only reflected in the earliest years of growth. Gaps in the shell-based record reflect declining growth rates through ontogeny as well as environmental tolerances. However, despite the presence of these gaps, when clams do grow they record high-resolution environmental variability. These results suggest that environmental reconstructions based on a single taxon, a single specimen or a single year may underestimate the full range of actual environmental variability. Therefore, to reconstruct the complete range of environmental conditions at a given locality several species, specimens and years may be required. This approach may be useful for reconstructing Pleistocene climates from western North America.

New sponge mimics from the Indo Pacific tropics

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Two new species of *Asteronotus* are described from the Indo-Pacific tropics. *Asteronotus mimeticus* sp. nov. is described from specimens collected in the Philippines, Palau, Australia, and Papua New Guinea. *Asteronotus spongicolus* sp. nov. is described from the three localities in Tanzania and one in northern Queensland, Australia. Both species are remarkably cryptic on their prey sponges. *Asteronotus mimeticus* is variable in its color and notal ornamentation, depending upon the sponge on which it is feeding. Both species differ from the only recognized species in the genus, *A. cespitosus* (van Hasselt, 1824) in their smaller body size, lack of regular ridges and rows of tubercles and differences in the radular morphology and reproductive system. The natural history, anatomy, systematic placement and biogeography of these species is reviewed.

Geographical and phylogenetic patterns of morphological diversity in strombid gastropods

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Strombids exhibit a wide range of shell morphologies. Adult body size is likewise highly variable (from 20 - 375 mm). Shell growth in strombids is determinate, allowing unambiguous identification of adult

specimens, including fossils. Geographically, we found that that the species richness of a region is a poor predictor of the morphological diversity present there. Areas with only a few species can harbor an impressive array of morphologies and, conversely, morphological diversity in the most species-rich regions is no higher than in regions with half their taxonomic diversity. To explore whether morphological patterns of disparity had a phylogenetic component, we used DNA sequences from mitochondrial (COI) and nuclear (H3) gene regions to infer relationships between 34 strombid species, including representatives of 9 of 11 named extant *Strombus* subgenera and all three *Lambis* subgenera. Our analyses suggest that despite its extreme morphology, *Lambis* is nested within the genus *Strombus*, a result consistent with its recent appearance in the fossil record. Thus, contrary to previous arguments, phylogenetic diversity is a poor proxy for morphological diversity.

Why life isn't always hotter south of the border: Latitudinal patterns in *Mytilus californianus* body temperature along the west coast of the U. S.

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Understanding the role of climate and climate change in driving the ecology of intertidal communities requires an explicit understanding of what the body temperatures of intertidal organisms are in the field. Because organism size, shape, and color all affect heat exchange, two organisms exposed to precisely the same climatic conditions can display very different body temperatures. These temperatures are also often quite different from the temperatures of the surrounding air and substrata. I deployed a series of temperature loggers that mimic the thermal characteristics of the competitively dominant mussel *Mytilus californianus* at sites ranging from northern Washington State (Tatoosh Island) to southern California (Santa Barbara). Results indicate that variability in temperature within any given site can far exceed that observed over a latitudinal gradient of several thousand km, due to the effects of substratum angle. Data further demonstrate that thermal stress does not increase monotonically along a latitudinal cline, and suggest the possibility of "hot spots" along the west coast of the U.S., where the timing of mid-day low tides coincides with extremes in terrestrial climate. Models of tidal exposure over the past 20 years indicate that these patterns change with time, and that we are entering a period where climate change is more likely to affect northern, rather than southern, sites. Supported by NSF IBN-9985878.

Paleo Eco-Devo: New perspectives on the evolutionary ecology of molluscan development

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Records of larval ontogeny on fossil mollusc shells have been influential in formulating paleoecological and macroevolutionary theory. Tests of theory have depended on using shells to infer the environment in which larval development took place, mode of larval nutrition, and length of larval life. Although recent studies have turned inward to the evolution of gene regulation of molluscan development, extrinsic factors continue to play an undisputed role in evolution of the larval phenotype. Fresh paleoecological insights arise from two sources: (1) detailed ontogenetic readings of biomineralized structure and (2) programs for integrating paleoecological, developmental, and evolutionary data.

Detailed reading of the gastropod protoconch shows that it is generated by different rules from the teleoconch. Materials chemistry and rules of self- organization provide new insight on the origin and evolution of larval shells. Metamorphosis is documented as sequence of events in which mineralization is reorganized. Details of reorganization in clades that infill the protoconch at metamorphosis and shed it as a directed ontogenetic event explain what previously has been considered preservational failure in the fossil record.

New patterns in the evolution of molluscan larval forms are revealed by plotting evolutionary trajectories through ecological and developmental spaces. A surprising result is the presence of multiple convergences on several regions of design space followed by within-clade decay back to ancestral ecological and developmental states.

Molluscan grazers on tropical rocky shores: The cause of spatially variable assemblage structure?

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Grazers are known to play an important role in assemblage structure elsewhere in the world, and may be responsible for the patchy distribution of sessile species on Hong Kong's tropical shores. Semi-exposed rocky shores in Hong Kong support a diverse guild of molluscan grazers that forage over a relatively narrow tidal range. Grazing pressure, as revealed by direct onshore observations of grazer activity and records of grazing marks on wax discs, is spatially variable at a scale of tens of ms. Such small-scale variation is linked to differences in the foraging patterns of molluscan grazers, some of which are restricted to refuges when immersed or emersed, and migrate upshore to feed whilst awash. It is also caused by the spatial heterogeneity (roughness) of the rock surface, as some grazers are more efficient in removing algae, cyanobacteria and settling stages of species at different scales of rock roughness than others.

Monthly exclusion experiments, replicated at different sites on the same shore, highlighted the spatial patchiness in grazer impact. While grazers are able to reduce the amount of erect algae and sessile invertebrates recruiting and growing on shores, this effect varies at scales of tens of ms. Patterns of species recruitment were more directly controlled by seasonal variation in physical stress and recruitment patterns, with grazing impact varying with season. This spatially and temporally variable impact of grazing pressure, when combined with patterns of species recruitment, results in the patchy distribution of sessile species seen on Hong Kong shores.

More than an artist: Olive Hornbook MacFarland's work to complete her husband's "Studies of Opisthobranchiate Mollusks of the Pacific Coast of North America"

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Olive Hornbrook MacFarland is best remembered for the stunning watercolors of live opisthobranchs which accompanied her husband Frank Mace MacFarland's studies of the opisthobranchs of the Pacific coast. Olive had always worked closely with Frank on his taxonomic work. They spent many a morning together tidepooling and hunting for new opisthobranch species. Olive took courses in Marine Biology and received her Master's degree from Stanford University in part to help improve her illustrations. After here husband died suddenly in 1951, Olive spent ten years assembling his beautiful treatment of the Pacific coast opisthobranchs. Together with his colleagues, she compiled all of his notes, drawings and a rough first draft of the monograph into the 550-page book, complete with 72 plates. A brief history of Frank MacFarland's work is presented, and Olive MacFarland's contributions to that work is detailed.

Preliminary phylogeny of the basal chromodorids (Mollusca: Nudibranchia)

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New collections of species of *Cadlina* and *Tyrinna* from South America and Antarctica have allowed for re-description of some previously poorly described species, have increased distribution records for some species and have yielded a number of new species. The general public's increased interest in dive

photography has added to our knowledge of the genus *Cadlinella* by expanding distribution records and documenting variation in members of this genus. Members of these three genera are unique in the Chromodorididae, in that they are found primarily in temperate and sub-tropical waters, have spicules in their mantle tissue, can have large tubercles and are for the most part white in color. In contrast, the rest of the chromodorids are primarily found in tropical waters, have smooth mantles and are brightly colored. Although it has been hypothesized that members of the genera *Cadlina, Cadlinella* and *Tyrinna* (the basal chromodorids) form a monophyletic group that is sister to the rest of the chromodorid nudibranchs, it has never been tested. I will present a preliminary species level phylogeny of this group based on morphological data.

Using underwater video for microacoustic and close-up non-destructive sampling near shallow vegetation around Monterey Bay.

(POSTER)

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Detailed, non-destructive ecological sampling has been largely impractical in shallow marine environments, where direct observations are laborious and can disturb the organisms excessively. Audio analyses of audible animal behaviors have been feasible with hydrophones, even in darkness or murky water. Modern, versatile video analyses (with audio) have become practical, especially for close-up observations. Common digital camcorders offer high visual and audio resolution, compact size, remote control, and (often) time-lapse capabilities useful in the lab and field. With hydrophones, audio-video records serve for documentation, illustration, and education about organisms and their numerous audible activities. These videotapes are a durable source of qualitative or quantitative data derived from scoring the sounds and images, often later. A flexible vinyl camcorder housing for many such cameras is inexpensive and compact. For depths, cost-effective housings sometimes fit a variety of camcorders. More elaborate housings enable external hydrophones, which provide instructive audio, often ignored. Some camcorders allow fixed audio gain, which is useful. Such records are providing a rare opportunity for long-term temporal comparisons, particularly in Monterey Bay, with its rich history of frequently sampled sites.

Convergence in the time-space continuum:
A predator-prey interaction

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Predation is a key structuring mechanism for some marine communities. Prey abundance may fluctuate with strength of predator recruitment and persistence except in cases where some of the prey population has a refuge in space or time from predation. The sponge *Halichondria panicea* is patchily distributed in the rocky intertidal of Kachemak Bay, Alaska, and in certain locations is the spatial dominant. This long-lived sponge is dispersed by planktonic larvae. At one site *H. panicea* dominated the mid-intertidal for over 10 years. Percent cover estimates show that *H. panicea* averaged 53% cover from August 1994-August 1996.

A major predator on *Halichondria panicea* is the nudibranch *Archidoris montereyensis*, which is also planktonically dispersed and has an annual life cycle. Total numbers of *A. montereyensis* at the study site ranged from 12 to 42 from 1994-1996. In the spring of 1997, strong recruitment resulted in an average population of 156 *A. montereyensis* on site from May to July. Percent cover of *H. panicea* declined from visual estimates of 40% in May to 15% in July. By August 1997, the sponge was absent at the study site. The number of nudibranchs declined to 7 individuals by September. Even though *H. panicea* is abundant in the region, providing numerous potential recruits, the site once dominated by *H. panicea* is now open rock heavily recruited by annual macroalgae. The predator-prey relationship of *A. montereyensis* and *H. panicea* is an example of a chase through space and time with convergence resulting in extreme population fluctuations and an unstable community.

Banana Slugs in a common garden: Reproductive parameters of *Ariolimax spp.* (Stylommatophora) in the laboratory

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The biology of the common giant slugs of the genus *Ariolimax* remains poorly understood. Five taxa have been described largely on the basis of genital morphology. Here we report the results of studies in which slugs from the various taxa were reared under the same laboratory conditions. Two taxa, *A. californicus* and *A. c. stramineus,* have been reared egg to egg in the laboratory with a generation time of 12 and 14 months, respectively. Hatching time is also similar between taxa; 6-8 weeks at ambient temperature. Otherwise, each of the taxa seems to have a unique combination of life history parameters. *A. columbianus* has large eggs (mean: 0.44 g), a high growth rate and (in preliminary observations) simultaneously reciprocal copulation with apophallation. *A. c. stramineus,* in contrast, has small eggs (mean: 0.19 g) and a slow growth rate. Its copulation has not been observed but it lacks apophallation. *A. c. brachyphallus* has medium sized eggs (mean: 0.26 g); its growth rate is unknown and preliminary observations indicate that it has unilateral copulation. Apophallation has not been reported for *A. c. brachyphallus. A. dolichophallus* has large eggs (mean: 0.44 g). a slow growth rate and simultaneously reciprocal copulation with apophallation. *A. californicus* has small eggs (mean: 0.16 g), a fast, variable growth rate and unilateral copulation in bouts.

Dangerous radicals and unsafe guides: A phylogenetic view of rocky shore communities

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Patellogastropods have been used worldwide in ecological investigations of rocky shore communities. They have limited morphological and ecological variation relative to other gastropods and are often treated as rocky shore “quinea pigs.” However, recent molecular and morphological phylogenetic

analyses are changing our view of their relationships and consequently requires a reevaluation of our understanding of rocky shore community composition, interactions, and history. Specific examples include the large, territorial limpet *Lottia gigantea*, and the marine plant limpets "*Tectura*" *depicta*, "*Tectura*" *alveus*, *Lottia alveus*, and *Lottia parallela.* Phylogenetic analysis also reveals subclade level patterns of range size as well as ecophenotypic plasticity, suggesting that current Pleistocene models of speciation are not likely for some groups. There is also pronounced asymmetries in diversity and ecology in several subclades. These reevaluations indicate that patellogastropod faunas are comprised of local radiations, invasions, and relicts, and that these different histories bring different sorts of evolutionary baggage with them. Being aware of these patterns will decrease the amount of variation in related studies.

Strangers in a strange land: What are we learning from biological invasions?

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Nonindigenous species are increasingly cited as pervasive and significant threats to native biodiversity, second only to anthropogenic habitat modification. Biological invasions act as "transplant experiments", providing ecologists with opportunities to study novel species interactions at several levels of biological organization. For example, Kellet's whelk (*Kelletia kelletii*) is a large subtidal gastropod whose northern geographic range limit recently expanded from Point Conception to Monterey Bay, California. Although the whelk was first recorded in Monterey Bay in 1980, the historical timeline of the invasion remains unclear, since one museum specimen was collected from Monterey in the 1960s. The fossil record provides a paleontological context, where conspecifics were found at least as early as the lower Pliocene in southern California, but not in central California. Field studies of populations in southern and central California suggest that timing of reproductive events is different, and the absence of annual recruits in central California, except possibly during ENSO events, may link reproductive success to sea surface temperature. As predators in central California, whelks are functionally novel, and feeding experiment results indicate novelty may be advantageous when handling naïve prey with ineffective anti-predatory defenses. As prey, whelks are primarily consumed by sea otters, a predator that has been absent from southern California for >100 yr. As sea otters expand southwards, abnormally high whelk populations are likely going to decline, which will impact any efforts to target this species for harvest, as has been suggested by the California Department of Fish and Game.

Odostomiine genera reconsidered: Shell characters versus spermatophore characters

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Robertson (1978, Biol. Bull. 155: 360-382, and subsequent papers) studied the biology of six species of Western Atlantic odostomiine pyramidellids of diverse shell morphology, finding that three species had large, shell-attached spermatophores and that another three species had smaller spermatophores positioned within the mantle cavity. Robertson (1978) used the genus *Fargoa* Bartsch, 1955, for the former group and proposed the new genus *Boonea* for the latter group, basing the classification chiefly on distinctions in the spermatophores. At the same time, he declared shell sculpture to be "unreliable in pyramidellid systematics." Robertson's classification has been followed by Wise in a series of recent papers and to some extent by Hori and his collaborators, whereas other recent authors have based odostomiine genera on shell characters, not commenting on the usage of *Boonea* and *Fargoa* for western Atlantic species. Using traditional methodology, in which I compare shell characters to those of the type species, my allocations for the species assigned by Robertson to *Fargoa* are: *Chrysallida dianthophila* (Wells & Wells 1961), in which genus the beaded axial ribs strongly project; *Fargoa bushiana* (Bartsch 1909), with clathrate, beaded sculpture in which the spiral cord above the suture is smooth and strongly projecting; "*Odostomia*" *bartschi* (Winkley 1909), with nearly smooth sculpture. For those species assigned to *Boonea* by Robertson, my allocations are: *Boonea seminuda* (C. B. Adams 1839), with evenly clathrate, beaded sculpture; *Oscilla impressa* (Say 1822), with strongly projecting spiral cords; and *Odetta bisuturalis* (Say 1822), with deeply incised spiral sculpture. The genera are broadly distributed and speciose. I argue that shell characters provide a multi-character data-set that is just as reliable for systematics in odostomiine pyramidellids as it is in any other family of shell-bearing marine gastropods. My hypothesis is that spermatophore differences serve as isolating mechanisms that enhance speciation within genera.

Progress toward completion of taxonomic reference manual: Shell-bearing Gastropoda of the Northeastern Pacific

(POSTER)

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Two volumes on shelled gastropods comparable to the highly acclaimed Bivalve Seashells of Western North America, by Coan, Valentich Scott and Bernard, published in 2000, are in advanced stages of preparation, to be published by the LACMNH. In order to provide reasonable geographic limits and to emphasize faunal distinctions and provincial radiations, the first volume treats the species of British Columbia to central Baja California and the second treats the more northern species of Arctic Alaska, south to British Columbia and west to the Kurile Islands, Russia. Type localities and type specimen repositories for nominal taxa and all synonyms, and citations of subsequent illustrations of type specimens are included, for the data-basing purposes of future workers. Most groups are subjected to major revision, bringing them into conformity with recent taxonomic advances. The format is sufficiently detailed to allow the descriptions of approximately 350 new species to be included in the text. Shells are to be illustrated in black and white on a white background, close to the text and with full captions. Although there has long been a demand for the Eastern Pacific gastropod book, and its importance to resource managers and modern systematists is evident, there are no calls for proposals from NSF or other federal agencies for the preparation of taxonomic manuals. However, I am pleased to report that the Packard Foundation has provided me with funding for an imaging technician, who is now preparing the plates from my negatives taken over many years. I do not have the benefit of a co-author, and the fauna is three times the number of bivalves, but with this help, there is now the expectation that the books will be completed.

Indo-Pacific Diversification: recurrent speciation at congruent boundaries

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The Indo-West Pacific (IWP) is the largest and most diverse marine region. The apparent wide species ranges, extensive sympatry, and great diversity that characterize IWP taxa have prompted diversification studies, but its origin remains unknown. Recent molecular evidence however indicates surprisingly structured populations in some taxa. We analyze the spatio-temporal pattern of diversification based on the first nearly comprehensive molecular phylogeny of a diverse, reef-associated group, cowries. We use a novel approach based on the geographic distribution of species pairs to test three models of speciation in marine organisms and find support for all three. Contrary to expectations, most (>95%) younger (~10 Ma) speciation events are geographically structured, implying that sympatric speciation is rare. We find that geographic barriers between allopatric sister groups occur widely. However, many cluster at the same oceanographic boundaries, but are discordant in time. These data refute simple vicariant mechanisms and support multiple vicariant or isolation by distance as primary mechanisms. Moreover, contrary to recent findings, speciation in the IWP is dominated by events occurring prior to Plio-Pleistocene eustatic sea-level fluctuations. These findings have implications for design of marine reserves that will capture the major elements of evolutionary processes in the IWP.

Sacoglossa bearing fusiform cerata from the Pacific coast of America

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Sacoglossa in the superfamily Limapontoidea Grey 1847 tend to be poorly defined because they are scarce, found in low densities and their prey algae is poorly known. Several species in our local fauna have been described by external features and the radula. Tooth shape is either blade (or awl) shaped or sabot shaped. In the late 70's and 80's, Tom Gasgoine published several papers emphasizing the

reproductive system. He divided into families those species with a more primitive hermaeid-type system and those with a more advanced stiligerid type. He postulated that these systems evolved from internal fertilization into a common female opening using a flagelliform penis. The seminal receptacle in these species is quite distant from the body wall. The use of a penial stylet and penetrant copulation evolved along with the movement of the bursa to a position against the body wall, often bulging the wall and sometimes forming an additional opening. This theory resulted in the transfer of several genera, notably *Placida* and *Alderia* to the stiligerid line. Unfortunately, both types of teeth can be found with both types of reproductive systems, which suggests that the sabot-shaped teeth have evolved in parallel. To clarify the generic placement of species along the eastern Pacific, I have dissected several incompletely described species with some surprising results.

Analysis of monospecific molluscan shellbeds: separating and extracting paleocological and taphonomic signals from Early Paleozoic bivalve accumulations

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INTRODUCTION

Bivalves first appeared in the Cambrian and diversified during the Ordovician Radiation approximately 500 – 480 million years ago. However, bivalves did not become major faunal elements in communities until much later in the Mesozoic (Sepkoski, 1981) and are thus considered members of Sepkoski's Modern Evolutionary Fauna. Today, bivalves are common important members of marine communities occurring in nearly every benthic environment that is not anoxic and are known at all depths from the intertidal to abyssal zones. During the Early Ordovician bivalves radiated on the western Gondwanan shelves (Babin, 1995) in siliciclastic (predominantly shallow-nearshore) settings within cool/cold water (subpolar) conditions (Babin, 1995; Cope and Babin, 1999). By the middle of the Ordovician, all major subclasses, reflecting all principal life-habit groups of bivalves, had undergone initial development on

Gondwana before radiating to other continents (Babin, 1995; Cope, 1997). During the Middle Ordovician, bivalves appeared in Baltica and Laurentia and by the Late Ordovician they were present in significant diversities in the warmer nearshore environments of Laurentia, Baltica and Siberia (Babin, 1995).

While the Ordovician Gondwanan history of bivalves is well documented, the nature of the global diversification is not. In particular, the Middle Ordovician bivalves of North America have been only anecdotally reported from about a dozen localities in the Great Basin (Pojeta, 1971; Li and Droser, 1999). Babin (1995) discussed Ordovician bivalve generic diversity and acknowledged only one Middle Ordovician genus, while Pojeta (1971) suggested that at least three genera may be present in the Great Basin during that time. In contrast, by the Late Ordovician, bivalve diversity on Laurentia had dramatically increased to at least 41 documented genera (Babin, 1995).

This study examines the paleoecologic, taxonomic, and taphonomic aspects of Middle Ordovician bivalves at six sites within the Basin and Range. The Lehman Formation outcrops at four localities within the Ibex region of western Utah (the Camp, K, L and Crystal Peak sections) and one locality at Steptoe, Nevada. An additional Middle Ordovician bivalve-bearing unit in southern Nevada is the Pogonip Group Member f of the Arrow Canyon Range.

Geological Setting:

During the Ordovician, the Great Basin was a near tropical carbonate platform (Ross, 1976; Ross *et al*, 1989; Droser and Sheehan, 1995). The bivalves at the six localities are all found associated with carbonate mudstones, occurring within successions of shallow water facies representing inner shelf and shallower marine environments (Ross, 1970, 1977; Ross *et al.*, 1989). Both stratigraphic units examined for this study are considered members of the Ordovician-aged Pogonip Group. The Lehman Formation is the uppermost member of the group, underlain by the Kanosh Formation and overlain by the Eureka Quartzite (Hintze, 1951). The Lehman Formation represents deposition in a shallow subtidal, likely restricted, environment. Micritic mudstones and wackestones are the dominant lithologies present throughout the unit. Terrigenous input increases up through the section and is expressed by a greater percentage of quartz grains in the matrix (McDowell, 1987).

The Pogonip Group cropping out in the Arrow Canyon Range is subdivided into six members, a to f (Langenheim *et al.*, 1962). The youngest, Member f, consists of argillaceous and silty limestones and dolomites. Lithofacies from Member f in the Arrow Canyon Range have been interpreted as intertidal to peritidal, with presence of oncolites in some beds (Stricker and Carozzi, 1973; Gunn, 1998). Langenheim *et al.* (1962) correlate Member f at Arrow Canyon with Hintze's (1951) Lehman Formation of Ibex based on similar lithologic and faunal characteristics.

METHODS

Although bivalves have been reported from several localities in the Basin and Range Province, this study focuses on the Lehman Formation and Pogonip Group Member f because bivalves appear in the greatest abundance in these units. Sedimentologic logs were produced for all of localities with particular attention given to the taxonomic and taphonomic composition of the fossil assemblages, in order to reconstruct in detail the depositional environments. Also general lithologies of the surrounding facies were noted and contacts above and below the bivalve-bearing units were examined and recorded.

Sedimentary and ichnological structures were examined and recorded at each outcrop. The relationship of size and abundance of body fossils to matrix (material less than 2 mm) were described. Packing and sorting of fossils within the units were determined using Kidwell and Holland's (1991) schematic scale of relative packing (densely packed, loosely packed, dispersed). Variations in packing and sorting distributions (both vertically and horizontally) throughout the units were described at each site.

In the field, paleontological observations were based on surface exposures (typically cross-sectional views). Fossil composition, diversity and relative abundance and the taphonomic condition of the fossils (including mode and quality of preservation) were described. Degree of ornamentation (*e.g.* presence of growth lines or tooth hinges) was noted, as well as the presence of articulated or butterflied valves. Multiple samples from each locality were collected for further laboratory analysis.

Petrographic information was obtained by examining thin sections from representative samples. Fossil abundance was determined through visual estimations of the percent-volume of fossils within the rocks using percent-volume charts, such as those provided by Schäfer (1969) and Kidwell and Holland (1991). Relative sorting and size variability of fossil material were also noted. In addition, petrographic analysis provided sedimentological information about the units, including matrix composition, ratio of grains to matrix, and relative abundance and size variability of inorganic (terrigenous) components of the rocks.

RESULTS

Sedimentology:

The Lehman Formation contains three repeating facies (tidal flat, nearshore, restricted), representing three distinct depositional environments. The base of the Lehman Formation contains two shallow water facies that repeat further up section. The first expression of this formation is interpreted to be a tidal flat environment. Within the tidal flat facies are densely packed ostracods are the only fossils present within this facies. Overlying the tidal flat facies are beds of cross-laminated sandstone, with microkarst surfaces, suggesting an intertidal environment of deposition. Bivalves and gastropods are uncommonly found in these beds and were not likely representative of an autochthonous community.

The remainder of the Lehman Formation is dominated by carbonate mud deposition and represents a restricted environment. Within this facies are two subfacies representing different depositional processes that have distinct paleontological and sedimentological characteristics. The first subfacies is a wackestone and packstone dominated interval interpreted to represent a shallow, restricted muddy setting periodically affected by storm events. The taxonomic composition of this subfacies is relatively diverse and is dominated by bivalves. Indeed, bivalves are found almost exclusively in this subfacies. The second subfacies consists of non-fossiliferous massive mudstone beds. This facies is interpreted to represent a subtidal muddy restricted environment Member f of the Pogonip Group outcropping in the Arrow Canyon Range has a similar lithology to that of the Lehman Formation and represents a shallow, subtidal muddy carbonate environment.

Paleontology:

Bivalves dominate the fauna in this setting in the Middle Ordovician beds exposed at Ibex, but other fossils are present. Gastropods, lingulids and uncommon orthid brachiopods are observed, along with rare ostracods (avg. 5 mm in size), cephalopods and trilobite pieces. Petrologic examination of some samples shows abundant small ostracods (<1 mm), comminuted ostracod shell material, and rare peloids within the matrix in addition to the macroscopic faunal components. Terrigenous grains are present, with fine silt-sized quartz grains (0.02-0.04 mm in size) comprising <5% to 20% of the matrix. Clay is also a prominent component in petrologic view, comprising up to 35% of the matrix.

The mode of fossil preservation, as well as the taphonomic condition of fossil material, varies between and within the four Ibex sites. Some of the bivalves are preserved as molds within the silty wackestones. For example, all of the bivalve specimens collected at the Camp and L sections are preserved as molds, with the original aragonitic material no longer present. Approximately half of these molds exhibit the traces of delicate growth lines. In contrast, all of the bivalves in the Crystal Peak section, as well as many of the specimens from the K section, are preserved as calcitic shell material, which weathers black in outcrop. Coarse recrystallization of this shell material is common, with millimeter-sized crystals observed on the shell surfaces. The black shells do not exhibit any fine detail, except rare tooth hinge structures.

On bedding plane exposures, it is difficult to determine whether the bivalve molds are articulated or single-valve representatives. Within the Camp Section, there are rare occurrences of the molds of butterflied shells and one example of what appears to be an articulated bivalve. At both the Crystal Peak and K sections, where bivalves are preserved as calcitic shells, there are several examples of articulated shells present in cross-section.

All of the Ibex bivalves can be identified as the modiomorphid bivalve, *Modiolopsis* sp. (Pojeta, 1971). Relatively well preserved specimens display the smooth contours of the shell, as well as hinge structures or growth lines, which greatly aid in the identification. Poor preservation (incomplete molds and coarsely recrystallized material) often prevents such specific identification. In these samples, such as all the L Section samples, only the general modiomorphid shape of the shells is preserved. Presence of *Modiolopsis* sp. in the Lehman Formation marks the first appearance of the genus on Laurentia.

The bivalves in the Lehman Formation most commonly occur in shell beds, and are uncommonly found dispersed in silty wackestones. Although sometimes found associated with other taxa, as discussed above, the bivalves are present most often in monospecific beds. They occur both as individual beds, and as amalgamated packages. These monospecific accumulations range from pavements to more than 20 cm in thickness. The bivalve beds are not particularly abundant, but are the most common shell bed greater than 1 cm in thickness in the Lehman Formation.

Some of the monospecific bivalve beds occurring in the muddy fossiliferous subfacies are thick, laterally extensive layers that can be traced over nearly 100 square kilometers. The shells in these concentrations are loosely packed and are oriented concordant to oblique to the bedding plane. There is no evidence of size sorting within the beds and most of the valves are whole, showing little abrasion or fragmentation. There are firm grounds and very little bioturbation. Bivalves of the Lehman Formation of Steptoe, in central Nevada, are found loosely packed within dark gray silty wackestone. Fossil material comprises 20-25% of the sample volume, with bivalves as the dominant faunal component. Gastropods and mud clasts are also observed. Petrographic examination of one sample from Steptoe reveals the presence of rare trilobite material, abundant shell fragments (~20%) and peloids (40%). Clay and fine silt-sized quartz grains are present in fossiliferous portions of the petrographic sample but are more abundant in unfossiliferous portions of the slide (up to 55%). The bivalves are typically preserved as black shell material on weathered surfaces and can be identified as drusy calcite in thin section. They are modiomorphid in shape but are too poorly preserved to identify more specifically.

In contrast to all of the Lehman bivalves examined in this study, the bivalves of the f Member of the Pogonip Group in the Arrow Canyon Range of southern Nevada are ctenodontid bivalves; close examination of acid-etched specimens suggests that they are members of the genus *Deceptrix* (Pojeta, 1971). Also, in contrast to the other bivalves presented in this study, the Arrow Canyon bivalves are preserved as silicified shell material that prominently weathers on outcrop surfaces. The ctenodontids are commonly the only macrofauna observed in the dark gray wackestone/packstone unit. They appear both in densely packed lenses and horizons (up to 60%), as well as dispersed shells within the unit (<10%). A few of the wackestone units underlying the bivalve-rich unit exhibit silicified fossil debris, which rarely includes bivalve material.

In the f Member in the Arrow Canyon range, bivalves are found in shell beds, as well as uncommonly dispersed in the surrounding mudstone and wackestone. Bivalves occur concentrated as lenses or pods, as well as in thin beds. The concentrations of bivalves at this locality occur most commonly as monospecific pods and beds. The shells in these assemblages are often whole or preserved as large fragments.

DISCUSSION

All of the Middle Ordovician bivalves examined in this study are found in silty wackestones to packstones associated with shallow marine carbonate facies. Sedimentologic, petrologic and paleontologic evidence in these units suggests that these fossil concentrations experienced minor transport. The Arrow Canyon and Ibex bivalve-rich horizons appear to have undergone mud winnowing, but not substantial fragmentation of the thin shell material. Petrologic examination of a sample from the Steptoe locality shows that the more fossiliferous horizons are essentially devoid of fine silt-sized grains (<5%) and tiny clay material (0%), whereas unfossiliferous portions contain up to 55% of the small terrigenous material. This may suggest slight winnowing of the more fossiliferous portions of the sample. Other Ibex units appear to represent relatively *in situ* assemblages. The butterflied and articulated shells present at Ibex sites indicate that the beds were only minimally exposed to taphonomic processes, suggesting that the bivalve-rich units represent relatively *in situ* or neighborhood assemblages. These dense concentrations of shells in pods are evidence of winnowing, but little fragmentation of the shell material suggests that they represent local or neighborhood assemblages.

Bivalves appear to be the dominant faunal component within the bivalve-bearing strata at all six sites. Faunal compositions vary from monospecific bivalve beds to bivalve-dominated assemblages, which include a variety of Ordovician taxa such as lingulids, orthid brachiopods, gastropods, ostracods and the rare trilobite and cephalopod. The Lehman faunal composition appears to be quite similar to bivalve assemblages of the Middle Ordovician of Avalonia (Cope, 1999). Comparison of the Avalonian fauna, which includes common lingulids, orthid brachiopods, gastropods and uncommon nautiloids and trilobites, to the Great Basin Laurentian fauna suggests that bivalves had established similar community structures in Avalonia before they moved to Laurentia in the Middle Ordovician (Cope, 1999).

Cope and Babin (1999) suggest that the scarcity of Middle Ordovician bivalves on Laurentia is "entirely due to the rarity of preservation of close inshore facies". However, data from this study suggest that Middle Ordovician bivalves were very common in certain types of nearshore settings, but had not been previously reported. The variety of taphonomic styles within the six bivalve-bearing strata examined in this study indicate that the apparent lack of bivalves is not simply due to taphonomic annihilation within nearshore environments. Further study of additional nearshore settings may reveal even more bivalves. However, clearly, bivalves were not as diverse at this time in Laurentia as they were elsewhere.

ACKNOWLEDGEMENTS

John Pojeta aided with the identification of the bivalve specimens. MLD acknowledges support from National Science Foundation (EAR-9219731). We also thank Roberto Falero for assistance in the field.

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Advances in the knowledge of the non-marine mollusks of Chiapas State, Mexico

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Through his study of the land and freshwater mollusks of the selva Lacandona, Bequaert (1957) brought together the information available on the fauna of Chiapas at the time. Later contributions were those by Thompson (1966) who described a new species of *Choanopoma*, and later (1967) a new species of *Linidiella*. In 1976, Thompson recorded a new species and subspecies of the genus *Epirobia*. The most recent publication is that of Naranjo-García *et al.* (2000) with the description of a new genus and species of a semislug (*Semiconchula custepecana*).

In 1993, Naranjo-García suggested that the terrestrial mollusks of Chiapas seemed to be rather different from most of the other states of Western Mexico; Sonora is also different. Some other interesting facts have emerged. First, after more than 150 years the semislugs *Xanthonyx chiapensis* (Pfeiffer, 1856) and *Simpulopsis simula* (Morelet, 1851) have yet to be recorded again. Second, *Semiconchula custepecana* from southern Chiapas belongs to a different branch of the superfamily Xanthonychoidea. And third, a single specimen of a slug from a high altitude forest belongs to a family unknown to me.

The updating and analysis of the non-marine mollusks of Chiapas will provide more information to corroborate the statement referred to earlier by Naranjo-García (1993). The non-marine mollusk material examined for this project is deposited in the Laboratorio de Paleozoología (INAH), Instituto de Biología (UNAM) and the California Academy of Science. The aim of this project is to provide a check list of the non-marine mollusks of Chiapas that will create a foundation for more in depth studies.

Inducible offenses: Phenotypic plasticity in feeding structures, food preferences, and dispersal potential in *Lacuna*, Family Littorinidae

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Although the evolution and ecological consequences of inducible defenses have gained a great deal of attention by scientists, inducible offenses have not. Like inducible defenses, inducible offenses are triggered by different environmental circumstances and increase performance of the individual. Inducible offenses include morphologies and behaviors associated with prey capture and consumption as well as competition.

Snails in the family Littorinidae have been found to have phenotypically plastic radular morphologies. However, to date, only those species in the genus *Lacuna* have been found to have inducible offenses, which include radular morphologies and feeding preferences. In addition, two species of *Lacuna, L. vincta* and *L. variegata*, show differences in dispersal potential as a function of feeding history. These inducible features could have large consequences for the population biology and ecology of these important herbivores and their ability to impact algal prey.

Feeding specialization in cryptobranchiate dorid nudibranchs: A review of hypotheses

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Nudibranchs are often assumed to be among the best-known marine feeding specialists, and are seen as a potential model system for testing hypotheses concerning the evolution of specialization. Yet Northeastern Pacific cryptobranchia (Nudibranchia: Doridacea) often have broad prey ranges comprised of numerous sponge taxa. How "specialized" are these slugs? Many common slugs have broad diets, with three or four prey species dominating at each site. These focal prey items change over the slug's geographic range, indicating some plasticity to diets. Nudibranchs are selective feeders, however, as prey use differs from availability within sites. Whether there are absolute prey preferences is unknown.

This range of dietary restriction contrasts with that seen in phytophagous insects and other "specialists," most of which have narrow diets comprised of closely related species, with relatively set preferences. Diets of many common Northeastern Pacific cryptobranchia show little taxonomic restriction and probably do not differ much in range or plasticity from those of other carnivorous gastropods. However, some cryptobranch taxa undoubtedly show narrower diets and, given their putative phylogenetic positions, hold promise as model systems for feeding specialization. Some hypotheses explaining narrow diet breadth seem relevant to these slugs (need for sequestered defense, available prey diversity), others possible (limited prey recognition, size and mobility), and a few are less likely (e.g., host-specific mating). Regardless, restricted prey range has probably evolved independently in several lineages of cryptobranchs, and the major influencing factors may differ among groups.

Morphological lumping and the generation of biases in paleobiogeographic and biodiversity analyses

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Paleobiogeographic distributions of molluscan taxa are being used increasingly as the bases for macroevolutionary, macroecological and paleoclimatic studies. The assessment of these distributions, or taxon ranges, however are derived largely from one-dimensional interpretations of the molluscan fossil record, namely first order rank taxonomic descriptions and taxon lists. Other important biological and interpretive sources of information, for example morphological, are generally ignored. This is a potentially important oversight since the taxonomic lists themselves are based commonly on non-quantitative or casual morphological assessments from localities beyond the site(s) of original and perhaps more careful morphological analyses. Yet it has been demonstrated repeatedly in the recent literature of fossil marine invertebrates that discrete morphological units exist within continuous taxon biogeographic ranges, and that these units correspond almost ubiquitously to distinct genetic entities with independent or divergent genealogical histories. Studies based on such taxon ranges may therefore grossly underestimate both biogeographic dynamics and estimates of biodiversity.

The possible extent of the problem is evaluated for Pleistocene and Recent venerid bivalves with putative ranges including southern California, the outer Pacific coast of Baja California, and the Gulf of California. Comprehensive geometric morphometric analysis of homologous landmarks provides the basis by which to assess both the levels and distributions of morphological variation within supposedly uniform species. The results will then be applied to descriptions of species ranges and changes in regional biodiversity over this geological interval.

Ecological and evolutionary responses of molluscan species to climate change

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Ongoing studies of biotic response to Pleistocene climate change have either focused on ecological aspects such as changes in species associations or on genetic changes. Morphological data have remained surprisingly neglected in this context despite the excellent Pleistocene fossil record of many vertebrate and invertebrate taxa. Analyses of Pleistocene and modern range limits of Californian marine bivalves show that body size plays a very important role in mediating species response to climate change. Similarly molecular phylogeographic analyses in conjunction with phenotypic measurements from living and fossil assemblages can provide important insights into the evolutionary responses of species and populations to climate change. Such integrative analyses not only provide insights into the evolutionary process but also have important implications for conservation of many species and populations. Mitochondrial sequence data in conjunction with morphological measurements from living and Pleistocene populations of *Acanthinucella spirata* show that exclusive dependence on genetic markers, as is the practice in most phylogeographic studies, only provides an incomplete picture of how these populations responded to climate change. But combining population level phylogenies with information from the Pleistocene fossil record reveals geographic areas where populations have seen rapid morphological evolution since the late Pleistocene. Clearly a better understanding of how species respond to climatic changes requires that we integrate ecological, genetic, morphological and paleontological data.

Biotic and abiotic factors control the invasion of introduced oysters

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What factors keep nonindigenous species scarce in portions of their introduced range? In this study, I compared abiotic constraints and biotic interactions at multiple trophic levels as they influence the invasion of Pacific oysters (*Crassostrea gigas*) in the NE Pacific. The experiment was set up at both wave-exposed and wave-protected sites to assess abiotic impacts. Potential predators and competitors were manipulated in a factorial experiment to assess biotic impacts of two guilds of native species on oyster growth and survival. Spatial variation in oyster abundance was related to wave exposure gradients, not species interactions, but oysters would be more abundant everywhere in the absence of intact native assemblages. The role of wave exposure in limiting invasion was evident from treatments lacking macroscopic native species: oyster survival was 33-69% lower and growth was 44-71% lower at wave-exposed vs. protected sites. The composite effects of two guilds of native species were similar in magnitude to abiotic effects. However, the guilds influenced oysters in different ways: predators reduced survival and neighbors reduced growth. Surprisingly, neighbors improved oyster survival, thereby facilitating one demographic variable related to invasion while restricting another. Finally, predators reduced oyster survival equivalently at wave-exposed and protected sites, despite being both more diverse and more abundant at the former. Together, these analyses affirm the importance of taxon identity in determining how native species influence invaders and indicate that biotic resistance may occur even in naturally species-poor communities.

A highly diverse Holocene invertebrate fauna collected after beach replenishment operations at Cardiff State Beach, San Diego County

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During the month of August, 2001 a phase of beach replenishment conducted by SANDAG (San Diego Association of Governments) transported ocean bottom sand from under 70 ft of water one km offshore to the shore at Cardiff State Beach. Shells contained in the sand were sifted out by the tides, and for approximately two weeks beginning August 19 repeated collections were made from this deposited material. Specimens were brought to the San Diego Natural History Museum, cleaned, sorted, identified and placed in the Paleontology Department collections. Two hundred fifty invertebrate specimen lots were entered, mostly bivalves and gastropods. Three vertebrates, including individual teeth of a bat ray, shark, and Sheepshead were also identified. The most common large gastropod, spread by the hundreds along the high tide line of the rocky berm, was *Bursa californica.* This species lives in shallow to deep water and shells usually are only occasionally brought on shore by winter storms. Other subtidal species common in the dredge material included *Turritella cooperi*, *Megasurcula carpenteriana*, *Terebra pedroana*, *Dentalium pretiosum*, *Pecten diegensis*, and *Glycymeris subobsoleta.* The specimens were empty and most were dull and slightly discolored. Although most specimens were probably derived from an offshore, buried Holocene deposit, a few of the subtidal shells brought up by the dredging were clearly modern. Among these were *Halistylus pupoides*, a few of which still had operculi in the apertures, and *Sinum scopulosum, Lucinoma annulata, Tellina idae* and other bivalves that still had periostracum attached.

To drill or not to drill? Ecology and evolution of a latitudinally variable predator-prey interaction

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The ecological and evolutionary forces that generate latitudinal variation in species interactions are poorly understood. We investigated predation by the rocky intertidal whelk *Nucella canaliculata* on the mussel *Mytilus californianus* at 16 wave-exposed sites along the coasts of California, Oregon, and Washington. From south to north, *Nucella* predation on this mussel changes from intense (south of Mendocino, CA), to weak (Northern CA and Southern Oregon), to nearly or entirely absent (Central Oregon coast), to stronger again (Northern WA). An identical pattern was observed when adult whelks from the 16 sites were held with *M. californianus* in the laboratory for >300 days. This striking and persistent variation in whelk predation could arise from prior conditioning to alternative prey, or through evolutionary differences among whelk populations. Because Nucella are direct developers, the potential for among-site differentiation is high.

To eliminate the possible effects of feeding history, we are quantifying the drilling behavior of whelks from different sites, hatched and reared on a common laboratory diet. To investigate the evolutionary history of these whelk populations we have sequenced 870 bp of a mitochondrial DNA gene (cytochrome c oxidase subunit I). Our data suggest some phylogeographic separation of weakly vs. intensely drilling populations, and high sequence differentiation among all whelk populations (few of the 39 unique haplotypes were found at more than one site). Thus, latitudinal variation in this whelk-mussel interaction may be driven in part by low gene flow among whelk populations, and spatially varying selection on drilling behavior.

A new species of *Tritonia* (Gastropoda: Dendronotacea) from Okinawa found to be feeding on a gorgonian (Cnidaria: Octocorallia)

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A new species of tritoniid nudibranch is described. *Tritonia n. sp.* is known only from Okinawa, at depths from 58 to 75 meters. Mature specimens are olive green in color, with lighter colored branchial plumes, nearly white rhinophores, and a thin white line along the notal margin. There are small low tubercles on all parts of the body, except for the foot. The oral veil is slightly bilobed and carries 12 to 14 elongate digitiform processes, many of which are apically bifid. There are 9 to14 pairs of branchial plumes. The rhinophore shafts are retractable, and are palmate in appearance. External genitalia, anus and nephroproct are on the right side of the animal. Buccal armature includes a pair of jaws with 2 to 4 rows of microscopic denticles along the masticatory border, and a radula with a tricuspid rachidian, a differentiated first lateral tooth, and a series of hamate to falcate lateral teeth. There are no cuticular plates within the stomach. *Tritonia n. sp.* has been observed to feed upon gorgonian octocorals of the family Ellisellidae (Gray, 1859), in particular *Verrucella aurantia* (Gray, 1869). Sclerites produced by the octocoral are isolated from nudibranch digestive system contents and compared with sclerites isolated from octocoral samples, providing further evidence of the association between *Tritonia n. sp.* and the octocoral family Ellisellidae. This is the first record of predation by a nudibranch on this family of octocoral.

Importance of bulk fossil sampling and community paleoecology in reassessing classic paleontological studies

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Paleoecology has undergone much change over the past 30 years, including the introduction of accessible, powerful, quantitative techniques. However, still important today is the collection of primary bulk fossil

samples from the field. Jurassic and Neogene examples of molluscan paleoecological analyses illustrate the misconceptions one can obtain when relying on literature or museum samples alone.

One previously discussed example includes population ecology studies on the Jurassic oyster, *Gryphaea.* Comparisons between specimens from museum, float, and bulk samples suggest that there can be very significant biases against small juveniles in collections: this bias greatly impacts demographic studies and life history interpretations. Other examples come from Neogene molluscan communities of the Dominican Republic. While specimens from these localities have played a prominent role in paleontology, no quantitative paleocommunity analyses have been conducted previously. With the collection of new bulk fossil samples, we have the opportunity to examine the ecological context of microevolutionary change. Preliminary observations of bulk fossil samples suggest that environmental and ecological shifts were occuring throughout the time interval, belying the notion of gradual environmental changes. Previously undocumented molluscan assemblages provide evidence for small-scale changes that cannot be detected by general facies and stratigraphic analyses. In addition, bulk fossil samples which have undergone no taxonomic, taphonomic or size sorting illustrate very dramatically the average small size of molluscan components and a high frequency of predatory behavior: observations not previously developed but which may have serious implications for the interpretation of Neogene Caribbean ecologies.

Does interspecific variation in the stress response limit distribution of intertidal *Tegula* species?

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Temperate to subtropical species of the genus *Tegula* occupy widely differing thermal environments from the subtidal to the mid-intertidal zone. We investigated possible mechanisms at the biochemical and molecular level that could limit the thermal niche of the various species. We focused on the heat-shock or stress response - which is characterized by the increased synthesis of heat-shock proteins (hsps) - because its properties have been shown to play an important role in setting the upper thermal limits of organisms. We studied the interspecific variation in the response, its regulation and its importance in setting limits to distribution ranges. Interspecific differences in onset, maximum and cessation temperature of hsp synthesis as well as in endogenous levels of hsp70s under laboratory and field conditions suggest that subtidal species are unable to inhabit the mid-intertidal zone due to their limited ability to cope with thermal stress. Additionally, the upper thermal limits of hsp synthesis may prevent temperate species from living in subtropical conditions. These interspecific differences are in part regulated by increasing amounts of the hsp-specific transcription factor (HSF1) in mid-intertidal species. This increase in "safety margin" may be energetically costly and could influence growth rates. Furthermore, differing levels of HSF1 in combination with interspecific variation in promoter sequences of hsp70 could ultimately be responsible for the differing stress responses and therefore for differences in thermal environment. Thus, it seems that biochemical and molecular aspects of the stress response are in part responsible for thermal limits that set distribution ranges.

Japanese sacoglossan opisthobranchs associated with *Codium* spp. (Chlorophyta)

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[3]Kominato Marine Laboratory, Chiba University, Japan

Diverse and abundant populations of herbivorous sacoglossan opisthobranchs inhabit Japanese rocky shores. We investigated sacoglossans that feed on the green macroalgae *Codium* spp. in Sagami Bay on the Pacific coast of Honshu, Japan. On the Miura Peninsula (eastern side of Sagami Bay), three sacoglossan species are particularly abundant: *Elysia trisinuata* Baba, 1949, *E. setoensis* Hamatani, 1968, and *Placida* cf. *dendritica* (Alder & Hancock, 1843). Phenology, population dynamics, and algal host use are described based on several short-term visits to Misaki Maine Biological Station (MMBS) and the literature. *Elysia trisinuata* grows substantially larger than sympatric sacoglossans on Codium by about two orders of magnitude (in wet weight). This sacoglossan mates and spawns in spring and small juveniles appear on algal hosts in summer. Juvenile slugs actively feed on *Codium* whereas adult conspecifics are presumed to rely on functional kleptoplasty. *E. setoensis* is extremely abundant on *C. fragile* in summer but does not form feeding aggregations or cause extensive grazing damage. *Placida* cf. *dendritica* is small, seasonally abundant on algal hosts, and causes algal host fragmentation and branch loss. These sacoglossan species frequently coexist on algal hosts, particularly *C. fragile*. Interspecific interactions appear be minor with no discernible interference or exploitation competition. The magnitude and potential asymmetry of sacoglossan interactions will be further explored.

Phylogeny of *Bathydoris*: changing dogmas in dorid nudibranch classification

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The traditional genus *Bathydoris* comprises 6 valid species, all of them found in polar or deep waters. An undescribed species from New Caledonia deep waters is clearly distinguishable from other members of the genus by having a triaulic reproductive system and a very elongated, spirally-coiled deferent duct.

A phylogenetic hypothesis of *Bathydoris* supports the monophyly of the Anthobranchia but shows that *Bathydoris* is paraphyletic. Species of *Bathydoris* are divided into two clades, one of them also containing the phanerobranch and cryptobranch dorids. *Bathydoris*, type species *B. abyssorum*, retains its name and diagnosis, but *B. clavigera* and the new species from New Caledonia are excluded from this genus. They are, however, provisionally maintained in "*Bathydoris*" *s.l.*, which is an artificial group. The other option is to introduce two new superfamilies to accommodate the two clades of "*Bathydoris*" *s.l.* This panorama shows some incongruities between the traditional nomenclatural system and modern phylogenetic systematics that could be resolved using a rank-free classification system.

Phanerobranch dorids: clade or grade?

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The Doridina, one of the four clades of Nudibranchia, traditionally comprises three major groups: Gnathodoridoidea, Cryptobranchia and Phanerobranchia. The monophyly of the Doridina is well supported by multiple sources (Wollscheid and Wägele, 1999). The Gnathodoridoidea, represented by the genera Doridoxa and Bathydoris, is the sister group of a clade including phanerobranch and cryptobranch dorids. Although the monophyly of the crypthobranchs has been already suggested (Wägele and Willan, 2000), the status of the phanerobranchs remains unclear. The phanerobranch dorids exhibit a large range of external morphology, colors, diets and internal anatomy (i.e., radulae and reproductive system). In an attempt to elucidate if phanerobranch dorids constitute a clade or a grade, we have sequenced the complete 16S mitochondrial gene for the majority of the phanerobranch genera and some of the cryptobranch genera. Phanerobranchs seems to be a non-monophyletic group in which are nested the crypobranchs.

Food preferences of mollusks and green algal secondary metabolites

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Temperate green macroalgae, particularly ulvoid algae such as *Ulva* and *Enteromorpha*, are often thought to be a highly palatable food for mollusks. However, using multiple-choice food-preference assays we found that the palatability of green algae is herbivore-specific. Some species, such as *Littorina sitkana* and *L. scutulata* preferentially consume some ulvoid green algae. Others, such as *Lacuna vincta*, preferentially consume brown algal kelps and avoid green algae. Most species of green algae produce an herbivore-activated chemical defense in which damage to the alga results in the conversion of

dimethylsulphoniopropionate (DMSP) to acrylic acid and gaseous dimethylsulfide (DMS). Mollusks that prefer green algae may be able to tolerate these defenses because they are not deterred by acrylic acid or DMS, or because the defense is not activated when the animals feed. In other mollusks, such as ascoglossan opisthobranchs, DMSP is taken up by the animals from the algae they are feeding on. These data suggest that the mollusks may use a variety of strategies to deal with green algal secondary metabolites.

Larval and adult ecology of Cambrian molluscs as a test of the DPC scenario

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In 1995, Davidson, Peterson & Cameron (DPC) suggested that the earliest bilaterians were, in effect, swimming larvae that were able to reproduce. They were forced to remain small (10^3-10^4 cells) because, perhaps like rotifers, they had not yet acquired the body-patterning mechanisms used to construct the sizeable adult bodies of most bilaterian metazoans. Thus, "maximal indirect development" via a trochophore-like larva was considered primitive for all Bilateria. However, the subsequent realization that all living bilaterians may be members of three major clades (Deuterostomia, Ecdysozoa, Lophotrochozoa) made the DPC scenario somewhat less likely; only the lophotrochozoans are characteristically indirect developers.

A second aspect of the DPC scenario is best addressed through the fossil record. Maximal indirect development involves a feeding larva that supplies raw materials to the rudiment (set-aside cells) that proliferate to generate the adult. Thus, an important test of the DPC scenario is the nature of development in primitive lophotrochozoans, the descendants of which now utilize maximal indirect development. If these animals lacked feeding larvae it would be difficult to argue for maximal indirect development being the primitive condition for crown-group bilaterians.

Cambrian molluscs are useful for this purpose. Their typically small adult body sizes and larval shell morphologies suggest that they were direct developers. However, their cosmopolitan geographic distribution, much broader than coeval trilobite faunas, argues for a planktic mode of dispersal. This is demonstrably not true for other early metazoans whose embryos are, remarkably, found in some Cambrian phosphate deposits.

The paleoecology of extinction

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Despite vast databases and a great deal of detailed work, and despite an imperative from conservation biology to study extinction events of the past, we still lack fundamental understanding of the ecological contexts of extinction. Using arguments from first principles and examples from recent marine biological history, with special reference to molluscs, I argue that those extinction events precipitated by disruptions to the productive capacity of ecosystems are far more destructive than are events precipitated by the evolution or immigration of overexploitative consumers. Although extensive work has clearly demonstrated that the addition or removal of high-energy consumers leads to major shifts in ecosystem structure and composition as well as to the extinction of some species, the extinction cascades triggered by disruptions in primary productivity are both more numerous and longer in duration. Such disruptions occurred during the Pliocene and Pleistocene in tropical America (especially the western Atlantic) and the North Atlantic. The major lesson from ancient extinction events is that the species most critical to the maintenance of ecosystems and their diversity are not top consumers, but primary producers — land plants, seaweeds, photosymbiotic animals, and especially phytoplankton — whose loss removes the food base and often the habitats for most species.

Barriers: where are they, how do they work, and what do they mean?

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With the advent of phylogeography — the geographical structure of populations — we have arrived at a new level of description in the spatial subdivision and classification of populations. We can now infer where parts of a population came from and potentially where barriers exist. From a conservation point of view, we can identify source and sink populations and infer geographical patterns of movement of individuals and genes. Beneath all the descriptive detail, the same questions arise that have occupied evolutionary biologists and biogeographers from the very beginning: what are barriers, how do they work,

and how do they change? Barriers prevent or limit the movements of individuals and therefore of genes. They may be imposed by physical regimes — unsuitable climates, patterns of circulation — or by contrasting biologically based selection, but in most cases, including many of the barriers identified in recent phylogeographical studies, we have no idea what the barrier is or how it works. As things stand, we tend to use character states as markers, and we appeal to the broad outlines of geological history and oceanography to identify past and present limits to distribution. Further progress hinges on integrating these lines of evidence with data on the economic and evolutionary contexts in which individuals and populations find themselves. I think the key is to identify the conditions — productivity, predation, competition — under which source populations thrive, and to specify when and under which circumstances individuals and genes from such source populations spread. I shall use the recent history of marine tropical America to illustrate these points.

Hot rocks and limpet clocks: Adaptations to life in the tropical intertidal

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The tropical intertidal is an extremely harsh environment, challenging species behaviour and physiology. The limpet, *Cellana grata*, is common on semi-exposed to exposed Hong Kong rocky shores. This grazer lives for ~ 2+ years and often suffers die-backs in the transition period from winter to summer. To survive this crucial period, and the stressful summer, *C. grata* shows a variety of responses. When inactive and emersed, it exhibits physiological responses such as variation in heart rate and haemolymph circulation to minimize problems of gas and heat exchange. When under intense stress, a mushrooming response (raising the shell from the rock surface) can occur which may permit short-term survival, but often culminates in a coma state or mortality. These responses are mostly important during low water emersion periods; however, the general behavioural rhythms of this animal are also vital to the maintenance of its optimal shore level, and hence survival. *C. grata* forages whilst awash, moving up shore with the flowing tide and down shore on the ebb, never becoming immersed by the tide. It stops movement and becomes inactive in the upper-mid shore in specific refuges such as crevices or vertical surfaces. Animals displaced higher than this tidal level, or out of their refuges, lose water rapidly, experience heat stress and die. The behavioural rhythm of *C. grata* is endogenously controlled by two clocks which firstly initiate activity, but secondly and most importantly act as a stopclock, therefore allowing this limpet to maintain its optimum level on the shore.

Seasons in the sun: A year in the Hong Kong intertidal

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Hong Kong lies within the tropics, yet experiences a strongly seasonal climate resulting in a wet/hot, tropical summer, and a cool/dry temperate winter, which greatly affect rocky shore assemblages. In winter, shores are covered by algal mats and ephemeral blooms of algae. Herbivorous molluscs are active over the entire shore and grazing by these molluscs and herbivorous crabs set algal distribution patterns. With the onset of summer, however, algae, grazers and many sessile species die-back or are restricted to refuges from physical stress. This transition can be quite sudden, associated with increasing air temperatures and a shift in tidal patterns. Typhoons also impact shores in summer, often scouring the rock surface clean. As a result shores can appear bare in summer, the only autotrophs being encrusting algae and cyanobacteria. Many grazers migrate down shore and are restricted to refuges (cracks and crevices). As such, biotic factors such as grazing pressure become relatively less important, except low on the shore, or under shade, where physical stress is reduced. With the onset of winter, as conditions ameliorate, algae recruit and grow rapidly, and biotic interactions become more important as grazers become less reliant on refuges. Small scale disturbance events within the seasons, therefore, have little long term effect on these shores, which appear controlled by physical changes in season. This strong climatic variation, therefore, has a great effect on the importance of biological processes and subsequent assemblage structure providing an interesting contrast to processes on less seasonal tropical shores.

Executive Board Meeting

The meeting of the Executive Board was held in the Triton Room, Asilomar Conference Center, Pacific Grove, CA, and was called to order by President Kitting at 4:05 PM, 20 July 2002. In attendance: George Kennedy, Chris Kitting, Roger Seapy, Cynthia Trowbridge, and Ángel Valdéz.

- Motion to approve previous minutes (M: Seapy; S: Trowbridge): accepted unanimously.

- Treasurer report (Trowbridge): the financial statement for the preceding year was reviewed and accepted for presentation at the Business Meeting (included in this volume)

- Nominating Committee report (Seapy): President: Ángel Valdéz, First Vice President: Jorge Caceres, Second Vice President: Peter Roopnarine, Secretary: Terry Arnold, Treasurer: Cynthia Trowbridge, Members at Large: Lindsey Groves and Edna Naranjo-Garcia.

  Motion (M: Kitting; S: Trowbridge) to accept the nominations presented by Seapy on behalf of the Nominating Committee: accepted unanimously.

- Student Grant Awards (report submitted by Hank Chaney and presented by Chris Kitting): The following students received awards: Christine L. Huffard, University of California, Berkeley -"The behavior and ecology of an undescribed member of the octopus (*Abdopus*) subgenus from Sulawesi, Indonesia"; Lisa Kirkendale, University of Florida - "Windows of opportunity: molecular phylogenetics and character trait evolution in the cardiid subfamily Fraginae"; and, Reuben Paul, California State University, Fullerton - "DNA sequence test of the lined chiton (Tonicella) species complex"

- WSMWeb Site: Valdéz reported that he will accept the responsibility for management of the WSM Web Site. The Board unanimously extended its thanks to Terry Arnold for his years of service to the society in that capacity.

- Old Business: status of the 2001 Annual Report was discussed by Seapy. He and Doug Eernisse are working to complete that report and, in combination with the 2002 Annual Report. They anticipate that both issues will be completed early in 2003 for printing and distribution to the membership.

- New Business: Kitting briefly reported on the financial resources from Cal State Hayward and from his own grants that provided support for the Symposia and student attendance. He also discussed the possibility of future joint meetings with AMS, although this would not be until after the 2004 World Congress in Perth, Australia.

- Reconvening of the Executive Board was requested by Kitting at a time to be determined during the course of the Annual Meeting in order to discuss possible avenues of collaboration with the California Malacological Society. (a lunch meeting was subsequently held on July 22 and proposals were discussed that would then be presented by Kitting at the Business Meeting)

Meeting adjourned at 5:40 PM

Respectively submitted,

Chris Kitting, with additions by Roger Seapy (for Terry Arnold, Secretary).

Annual Business Meeting

The Annual Business Meeting of WSM was held in the Surf and Sand Meeting Room, Asilomar Conference Center, Pacific Grove, CA on 23 July 2002. The meeting was called to order by President Kitting at 5:20 PM.

- In recognition of help he received in putting on the meeting, Kitting acknowledged the following people: N Franceschini, C. Duncan Kitting, C. Davis, and E. Hawkes from CSU Hayward, C. Trowbridge from Oregon State University, and R. Seapy from CSU Fullerton. Kitting also extended his gratitude to the San Francisco Bay Wildlife Society and other Symposium fund sources, including UC Berkeley Museum of Comparative Paleontology.

- Web site update: on behalf of the society, Kitting thanked Terry Arnold for his many years of service in the capacity of web site manager. Kitting then announced that Ángel Valdéz had accepted the responsibility for development and management of the site through his position at LACMNH.

- The Treasurer's Report (included in this volume) was submitted by Treasurer Cynthia Trowbridge and reviewed at the Executive Board meeting. The Report was presented to the membership by Kitting. A brief discussion followed regarding the status of donations from shell clubs.

- The Nominating Committee Report was presented by Roger Seapy, Chair. The slate of nominees for 2003 included: President - Ángel Valdéz, First Vice President - Jorge Caceres, Second Vice President - Peter Roopnarine, Secretary - Terry Arnold, Treasurer - Cynthia Trowbridge, and Members at Large - Lindsey Groves and Edna Naranjo-Garcia.

  With no additional nominations for these positions, Kitting called for a vote to approve the slate of nominees, with gratitude to Seapy and his committee. The nominees were accepted unanimously.

- The Student Grants Committee Report was submitted by the Chair of the committee, Hank Chaney, and presented by Kitting. The following students received awards: Christine L. Huffard, University of California, Berkeley –"The behavior and ecology of an undescribed member of the octopus (*Abdopus*) subgenus from Sulawesi, Indonesia"; Lisa Kirkendale, University of Florida - "Windows of opportunity: molecular phylogenetics and character trait evolution in the cardiid subfamily Fraginae"; and, Reuben Paul, California State University, Fullerton - "DNA sequence test of the lined chiton (Tonicella) species complex".

  A motion was made by Kitting to approve the report of the Student Grants Committee, contingent on new donations from shell clubs to be solicited and acknowledged. The motion was approved unanimously.

- Plans for the upcoming 2003 meeting of the society at the Los Angeles County Museum of Natural History were presented by Ángel Valdéz. The dates of the meeting are 6 – 10 June 2003. Three symposia are tentatively scheduled and field trip options are being developed.

- Kitting announced that the 2004 meeting of the society will be held in Ensenada, Mexico, and will be organized by the incoming First Vice President, Jorge Caceres.

- The Editor of the Annual Report, Doug Eernisse gave a brief update on the status of the 2001 Annual Report (currently in preparation) and anticipates completion of both that report and the one for the current 2002 meeting in early 2003.

- New Business: the opportunity to enter into a collaborative arrangement between WSM and the California Malacological Society (CMS) was discussed by Kitting. Kitting indicated that a major benefit of such an affiliation would be to greatly increase the visibility and status of WSM. Several options for collaboration were presented, of which the major one was sponsorship of one issue of the Veliger each year by WSM. The society would encourage the submission of manuscripts based on presentations made at meetings of the WSM for publication in that issue. A vigorous discussion ensued, which largely revolved around the question of long-term financial committments to any form of collaborative agreement. A motion was made and approved unanimously to table the discussion, with the recommendation that the subject be referred to the Executive Committee.

- Kitting handed over the remainder of the meeting to the incoming President, Ángel Valdéz.

- A proclamation was voiced to acknowledge the contributions of Kitting and his staff of assistants for an outstanding job at organizing and carrying out the 2002 Annual Meeting at the Asilomar Conference Center.

- The meeting was adjourned at 6:30, followed by the Group Photo (included in this volume).

Respectively submitted,

Chris Kitting, with additions by Roger Seapy (for Terry Arnold, Secretary).

TREASURER'S REPORT

1 October 2001 – 30 September 2002

INCOME

Membership Dues *		
Dues 2001	90.00	
Dues 2002	1602.00	
Dues 2003	15.00	
Dues 2004	15.00	
Total Dues		1722.00
Student Grant Donations *		
Santa Barbara Malacol. Soc.	500.00	
WSM Members	175.00	
WSM Reprints	13.10	
Total		688.10
Symposium Fund Donations		88.00
Student Travel		115.00
Royalties		141.97
Meeting Income		5150.53
Interest Income		20.21
Total Income		**$7925.81**

EXPENSES

Administrative Costs	
Non-Profit Corporation	20.00
Reciprocal Dues	20.00
Mailing/Photocopying	107.89
Total Administrative	147.89
2002 Student Grants	1700.00
Annual Report 2000	
Printing Costs	371.29
Mailing Costs	0.00
Total Report Costs	371.29
Meeting Expenses *	6186.31
Total Expenses	**$8405.49**
Net change	**-479.68**
Balance brought forward 10/1/02	**$14108.31**

ASSETS

Savings (does not include all of current interest)	
CD 28667-10492 (matures 12/05/02)	3217.51
CD 28660-11699 (matures 11/16/02)	4000.00
Total	**7217.51**
TOTAL ASSETS	**$21325.82**

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* Some dues for 2002, donations for 2002 student grant, and expenses for 2002 occurred after 30 September 2002.

Student Grant Activities

The following students are the recipients of the 2002 WSM Student Grant Awards:

Christine L. Huffard, Department of Integrative Biology, University of California, Berkeley
"The behavior and ecology of an undescribed member of the Octopus (*Abdopus*) subgenus from Sulawesi, Indonesia" - $850

Lisa Kirkendale, Department of Zoology, University of Florida, Gainesville, FL
"Windows of opportunity: molecular phylogenetics and character trait evolution in the cardiid subfamily Fraginae" - $850

Reuben Paul, Department of Biological Science, California State University, Fullerton
"DNA sequence test of the lined chiton (*Tonicella*) species complex" - $500

The Student Grants were made possible by the generous contributions of the following:

Individual donations from members of WSM
Northern California Malacological Club
San Diego Shell Club
Santa Barbara Malacological Society
Southwest Shell Club
Western Society of Malacologists

Rows are irregular and the corresponding names for each row are listed from left to right:

Front Row (sitting): Roger Seapy, Jim Nybakken, Ángel Valdéz, Chris Kitting, Ann Knowlton, Edna Naranjo, Jamie Chan, Wallis Chan, Audrey Aronowsky, Diana Boyer.

Middle Row (kneeling and sitting): Carole Hickman, Jeb Byers, Mary Jane Adams, Rebecca Johnson, Kinsey Frick

Back Row (standing): Lance Gilbertson, Cheryl Davis, Charlotte Norrid, Roma Metz, Walter Carr, Steve Lonhart, Carole Hertz, Janet Leonard, Mike Ghiselin, Liz Hawkes, Jules Hertz, Brooke Weaver, Kirstie Kaiser, George Kennedy, Benoit Dayrat, Neil Hutchinson, Doug Eernisse, Sandra Millen

Individual Memberships

ADAMS, Mary Jane, 2116 Canyon Rd., Arcadia, CA 91006-1505
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